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The Role of Copper in Plants and Its Uptake and Assimilation by Plants

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Role of copper in plants

Copper (Cu) is an essential micro nutrient which is necessary for the development and growth of plants. For healthy development, plants generally require 5-30 mgkg^{-1} Copper (Wuana and Okieimen, 2011). Cu acts as a cofactor for several metal proteins and is a key player in several physiological and biochemical processes. In several regulatory proteins, copper is a structural constituent and plays a key role in several reactions such as cellwall metabolism, protein metabolism, photosynthetic electron transport, hormone signaling, oxidative stress responses, mitochondrial respiration, and ethylene sensing (Zhang*et al.*, 2019). The most important role played by Cu in plants is electron transport reactions in mitochondria and chloroplast. In numerous electron carrier proteins copper is incorporated as a structural component. Plastocyanin is an electron carrier protein in light reaction of photosynthesis engaged in the transport of electrons from cytochrome f to P700+.Plastocyaninaccounts for nearly 50% of the Copper present in the chloroplast. Copper have the capacity of gaining or losing electrons easily, therefore serving as a co factor of several enzymes such as Cu/Zn superoxide dismutase, amino oxidase, cytochrome c oxidase and polyphenol oxidase (Nazir *et al.*, 2019)

Plants need to maintain ideal quantities of copper in various tissues for optimum growth and development. Copper deficiency results in the development of various symptoms in plants such as stunted growth, reduced growth rate, chlorotic symptoms, photosynthetic electron transport chain damage, curling of leaves at margins, reduced fruit formation, chlorosis of young leaves and dieback of stems. Under copper deficiency synthesis of plastocyanin is reduced and PSII activity is inhibited (Thomas *et al.*, 2016). Copper has an important role in carbohydrate and nitrogen metabolism, so under copper deficit conditions plants become stunted. Further, Copper is required for the biosynthesis of lignin which is required for cell wall strengthening and prevention of wilting. Cu deficiency induces damage to the photosynthetic apparatus and it leads to the generation of oxidative stress. Light energy absorbed by photosynthetic pigments is redirected to produce reactive oxygen species (Shabbir *et al.*, 2020). Under Cu deficiency, Cu/Zn-SOD activity is severely hampered which is involved in converting more harmful superoxide radicals to less harmful hydrogen peroxide.

Uptake of Copper by Plants

Cu is present in two oxidation states they are +1 (Cu^+, cuprous ion) and +2 (Cu^{+2}, cupric ion).The most common oxidation state of copper is a cupric ion. In the soil, Cu is present as free ions, precipitated forms, and exchangeable forms, organic and residual forms. Copper is used to accumulate mostly in topsoil as it is less mobile in soil. Due to its high affinity towards the organic matter, Cu leaching rate is lessso and it accumulates in the soil (Kumar*et al.*, 2021).

Only a part of the total metal pool present in the soil is accessible to plants. The Phyto availability of copper depends on soil properties and plant-specific factors, which regulate Cu mobility and availability in the soil. Plants mainly uptake copper in the form of Cu^{2+} and Cu^+, and the mobility of these ions is dependent on soil properties such as pH, organic matter, etc. The epidermal root cells of plants absorb copper ions from the soil matrix, which are then transported via the parenchyma and endodermis, and finally enter the xylem. The mechanisms of the acquisition of copper have not been fully deciphered yet. Copper uptake from root involves a mechanism of reductive uptake of $Cu^+$from Cu^{+2}at the root cell surface. Cu^{+2} chelate reductase enzyme reduces Cu^{+2} at the surface of the root. This enzyme wascoded by the ferric reductase oxidase gene (*FRO4/5*) (Kumar *et al.*, 2021).

Heavy metal transporters involved in copper uptake

P-type ATPase copper transporters

The P-type heavy metal transporters facilitate the movement of metal ions such as Cu^{2+}, Zn^{2+},Pb^{2+},andCd^{2+}.They are divided into the 1A ATPase and the 1B ATPase groups. 1B ATPase can be categorized into two classes based on genes code for the transporters, i.e.,divalent cation transporters and monovalent cation transporters. Eight members of the type 1B family are found in the genome of rice and Arabidopsis, and they are known as

HMA1 to HMA8. Synthesis of ethylene receptors requires copper which comes from the secretory pathway. HMA7 is the key player involved in the transfer of Cu to secretory pathways. HMA6 is involved in the transport of Cu to the chloroplast where copper acts asa cofactor for the Cu/Zn SOD enzyme.*OsHMA4* gene identified in rice plants regulate Cu acquisition in rice grains (Huang*et al.*, 2016).

COPT copper transporters

COPT transporters are a major family protein, which regulates the transportation of Cu in reduced form. Expression of COPT1, COPT2, and COPT6 was increased under Cu deficit conditions. The COPT1 transporters are situated on the plasma membrane of cells, especially at the root tips. They are primarily responsible for the uptake of copper from soil and they have a high affinity for Cu^+. Under Cu limited conditions, the expression of COPT1 upregulated there by helping in the increased acquisition of Cu from the soil matrix. The COPT2 is mainly expressed in the root epidermal cells and root hairs. Additionally, COPT3 and COPT5 have a moderate rate of Cu affinity and transportation. These transporters may involve in the indirect transport of Cu through a secretive pathway (Kumar *et al.*, 2021).

ZIP family transporters

ZIP family transporters (zinc-iron regulated protein transporters) are involved in the regulation of the uptake of copper. The transport of Cu ions is based on the availability of copper in the growing medium and their transport is mainly through ZIP4 and ZIP2 transporters. The expression of genes encoding for ZIP4 and ZIP2was upregulated under Cu deficiency conditions and down regulated under excess copper availability (Milner*et al.*, 2013).

NRAMP family transporters

The Natural Resistance Associated Macrophage Protein (NRAMP) transporters are mainly involved in the relocation of metal ions such as Fe, Zn, Mn, Ni, and Cu

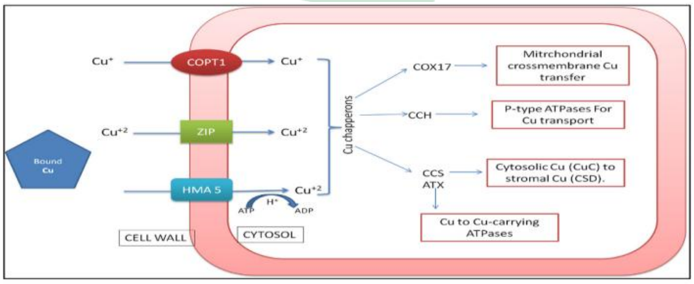

Figure: Different transporters and Cu chaperons involved in uptake and sequestration

These transporters assist in the transfer of harmful metal ions across cell membranes and vacuolar membranes in plants (Kumar *et al.*, 2021).

Copper Translocation and Sequestration in Plants

Specific metal chelators and transporters mediate the transport of Cu to aerial plant parts from the root. Cu chaperons are low-molecular-weight receptors present in the cytosol and they facilitate the translocation of metal ions across membranes within the cells. These chaperones assist in the delivery of Cu ions to the active sites of enzymes that require Cu as a cofactor. Thereby Cu chaperons prevent the interaction of copper with any other moleculesin cells (Markossian and Kurganov, 2003).Mainly three major types of Cu chaperons are identified, they areCCS, CCH, andCOX17. The CCH regulates the transfer of Cu to Cu-carrying ATPases. The CCH binds to the Cu^+ and interacts with the P-type Atlases and thereby facilitating Cu transportation. Expression of plant CCH depends on the plant aging and oxidative stress status in plants. Stromal CCS assists in the transport of Cu to PAA, which is mainly involved in the transfer of cytosolic Cu to stromal Cu. COX17 mediates the transport of Cu across mitochondrial membranes (Printz *et al.*, 2016). The transport ofcopper to mitochondria is mediated by AtCOX17, where Cuis used as a structural component of the cytochrome oxidase complex.

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